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**Megafauna Extinction:  
A Paleo-economic Theory of Human Overkill in the Pleistocene\***

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**Abstract:** After centuries of debate, paleontologists are converging towards the conclusion that human overkill caused the massive extinction of large mammals in the late Pleistocene. This paper revisits the question of megafauna extinction by incorporating economic behavior into the debate. We allow for endogenous human population growth, and labor allocation decisions involving activities such as wildlife harvesting and (proto) agriculture. We find that the role of agriculture in deciding the fate of megafauna was small. In contrast, the presence of ordinary small animals that have been overlooked in previous non-economic extinction models is likely to have been much more important.

**Keywords:** Megafauna collapse, early humans, climate change, hunting

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## 1. Introduction

About 12,000 years ago one of the great scientific mysteries occurred. Up until that time, during the first two million years of the Pleistocene, species rarely went extinct. In the Americas, for instance, fifty species of large mammals went extinct, an average of 1 every 40,000 years. But then around 12,000 years ago something changed, and over the next two thousand years, species extinction exploded. The Americas lost fifty-seven large mammals, including three genera of elephants, in this short time span, an average rate of *1 every 30 years*. Megafauna such as mammoths, mastodons, giant ground sloth, and *Deinotherium* disappeared, and many agile species like horses and camels went extinct locally.

Centuries of debate within the palaeontology community over megafauna extinction have produced two competing theories, climate change versus human overkill. The climate change view argues that megafauna extinction occurred because large species were slower to adapt to advancing and retreating ice sheets than the plant communities upon which they grazed. The plants adapted relatively quickly to abrupt climate change; the large mammals did not, hence their exit.<sup>1</sup> The theory of human overkill counters it was early man with his limited technology, not climate, that created havoc in the natural world. In the Americas, for instance, evidence suggests the small bands of Clovis people crossed the Bering land bridge from Asia about 12,000 years ago.<sup>2</sup> The fact that species began to disappear abruptly at the same time, so the argument goes, was no coincidence. Some fossil evidence exists to support the view that skilful hunters preyed on large mammals that did not adapt to their new and aggressive predator.<sup>3</sup>

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<sup>1</sup> While at first appearing logical, some observers have noted the theory does not explain what was unique to the end-Pleistocene retreat of the icesheets. Warm interglacials were not uncommon in the Pleistocene and they were never accompanied by such faunal losses before.

<sup>2</sup> Archaeologists have named the Clovis people after the site where their projectile points were first unearthed in 1927 in Clovis, New Mexico. Accumulating evidence now suggests that perhaps Clovis people were not the first humans to set foot on America, but this is irrelevant for the purpose of the overkill hypothesis. They were likely the first to reach appreciable numbers and occupy sizable territory.

<sup>3</sup> Because human hunters and wildlife have co-evolved in Eurasia and Africa (presumably resulting in less naïve wildlife), it is claimed that extinction due to overkill is not nearly as pronounced as in the Americas and

Many natural scientists believe it is essential to understand today whether it was climate or primitive man that caused the megafaunal collapse. Such knowledge provides a history lesson on what might happen in the future if we do not address modern risks of climate change and overpopulation (see, e.g., Leakey and Lewin 1995), but at least until recent times, progress in understanding what happened has been hampered by an identification problem, at least in North America, megafauna extinction occurred both when man first appeared and during a violent phase of climate change. Both forces hit the megafauna simultaneously, and the fossil record has provided little help in differentiating between the hypotheses due to the simultaneity issue and poor quality fossil data.

Two recent well-publicized studies examining extinctions in Australia and in the Americas, however, point to human overkill as the culprit. For Australia, Roberts et al. (2001) found the continent-wide extinction did not coincide with extreme climatic events, implicating overkill as the most likely explanation. For North America, the paleontologist Alroy (2001) followed others who have used mathematical simulation to explore the plausibility of the theories (e.g., Mossimann and Martin 1975, Whittington and Dyke 1984). Using a model that was much richer in ecological detail than prior analyses (e.g., he distinguishes between 41 herbivore species rather than one aggregate stock) and relaxing some restrictive assumptions that had been made by others (e.g., constant human population growth rates), Alroy points to overkill as the culprit. Although these studies have not ended the debate over climate change versus overkill (e.g., Brook and Bowman 2002, Stuart 2005), they do suggest growing support within the paleontological profession for the theory that, at least in North America and Australia, human overkill is responsible for large-scale extinction of megafauna.

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Australia. Many of the megafauna surviving the collapse in the Americas (e.g., bison, moose, elk, musk ox) were themselves migrants from the “old world” and presumably better adapted to avoid man’s predatory habits.

But the overkill explanation raises an important set of new questions. If overkill was the cause, why did it happen? And what economic behavioral mechanisms could have driven this result? Unfortunately, these paleontological models cannot address these questions because they lack a realistic behavioral component. Rather these models tend to be “fully mechanistic,” with humans as “super predators” who spend their time either hunting or procreating. More specifically, these paleontological simulation models focus exclusively on megafauna hunting and do not address the broader opportunity set and the behavioral tradeoffs facing households in the late Pleistocene. In effect, these models sidestep Smith’s (1975) durable point that the separation of man and nature does not address primitive man’s labor allocation decisions (for example, whether to hunt megafauna or spend time in other activities), and this choice could affect the degree to which overkill played a role (see also Shogren and Crocker (1999) on the issue of nature and economics being jointly determined). Smith argues, and we agree, that explicit economic behavior should be considered “to demonstrate the use of a coherent economic framework for the study and evaluation of extinction or other hypotheses concerning the primitive hunter culture” (1975, p.750).

This paper explores the plausibility of the overkill hypothesis and examines the economic mechanisms that might support this hypothesis. Overkill is only consistent with megafauna collapse *and* human survival if humans have access to a substitute food source (i.e., an outside option). Otherwise, humans would die after the megafauna go extinct. Smith (1975) suggests agriculture provided the substitute food source and was the impetus of megafauna extinction. But this theory has yet to be tested in a model with endogenous human population growth, and a numerical analysis has never been performed to examine the robustness of the theory. Extending Smith (1975), we develop and calibrate a model allowing for endogenous growth of both animal and human populations (see Nerlove 1993),

in which a hunter allocates his labor between alternative uses given an endogenous species kill rate.<sup>4</sup>

We find that Smith's case for early agriculture can be challenged as the likely explanation for megafauna extinction. Such proto agriculture may let the human population grow faster, which could increase hunting pressure on megafauna, but a competing opportunity cost effect emerges because the ability to subsist from plant-based food increases the opportunity cost of hunting for scarce animals, certainly when animal stocks are small and catch per unit of effort is low. By introducing a lower bound on the opportunity cost of hunting effort, agriculture could *decrease* the likelihood of megafauna extinction. Our numerical results indicate the opportunity cost effect was likely sufficiently strong to avoid megafauna collapse, which does not support agriculture as the cause of extinction.

If agriculture was not the cause, what was? We propose the cause was a second alternative food source, *small animals* or “mini-fauna.” As people allocate more effort to hunting minifauna, more opportunities for chance encounters with megafauna arise, which leads to more megafauna harvests. In contrast, if labor is devoted to agriculture, opportunities for chance encounters decrease. Hunting minifauna is a complementary activity for megafauna harvests, whereas agriculture is a substitute activity. Moreover, if overkill occurs in the presence of a steady supply of substitute prey, mainly the small and ordinary animals living today, these minifauna could have supported human population growth when megafauna became scarce. Small and rapidly replenishing animals such as deer can support an expanding human population, even as megafauna densities fell. The incidental killing of megafauna continued until extinction occurred, and humans moved on. While our results support Alroy's mechanistic findings that many smaller animals survived while the larger ones were killed off, our behavioral model captures endogenous feedbacks

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<sup>4</sup> Evidence suggests there were no more than 200 to 400 Clovis people entering Canada some 12,000 years ago (Whittington and Dyke) which suggests understanding the dynamics of the human population is crucial to

between the economic and natural system and triggers results that point directly at humans as the culprits of megafauna extinction.

The organization of the paper is as follows. In section 2 we consider the case in which people allocated their time to either hunting megafauna or agriculture and numerically demonstrate that such a model is not consistent with megafauna collapse. In section 3 we expand the model by adding small animals ("minifauna") as an alternative prey base. While agriculture is a substitute activity for hunting megafauna, minifauna hunting is arguably a complementary activity. Megafauna overkill is a robust outcome for such a model. The conclusions ensue in section 4.

## **2. Megafauna harvesting and proto agriculture**

Imagine a group of primitive hunters, consisting of  $N$  identical households. These people sustain themselves by consuming food,  $F$ , which comes in the form of meat from megafauna (mammoths, mastodons, giant bison etc.),  $m$ , and also plants (e.g., nuts, berries, grains),  $p$ , that come from proto agricultural activities. Some additional gathering may have occurred in combination with hunting (the combination of activities is also known as 'foraging'), but we ignore this and assume the hunting lifestyle in the late Pleistocene yielded meat as the edible output (an assumption supported by Mosimann and Martin). This leaves early agriculture as the source of plant-based food.

Several theories attempt to explain the transition from hunting/foraging to agriculture. Early theories were based on the assumption that the quality of life for hunter-gatherers was poor and governed by brutal Malthusian processes. In light of anthropological evidence that hunter-gatherers were healthier and less over-worked than early agriculturalists (e.g. Angel 1975, Diamond 1992, Haviland 1993, Megarry 1995), this perspective started to change. There has been a period of some 7,000 years (the so-called Mesolithic) that, according to

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understand the potential for overkill.

Marceau and Myers (2005), may be characterized as a “transitional and unstable period of broad spectrum foraging and the earliest agriculture.” While proto agriculture emerged independently in a number of dispersed locations in the world within a few thousand years, evidence also exists that hunter-gatherers lived side-by-side with farmers (Cashdan 1989). This suggests a gradual transition and, likely, an element of occupational choice and specialization by humans. The various modern theories of the transition differ in the causal mechanism that is identified as the trigger of the rational choice to abandon hunting/gathering (e.g. technical change, institutional change, environmental change, population growth), but they share the common feature that there was a food crisis. We capture the relevant tradeoffs in a stylized way by developing a conventional economic model of rational choice, but we emphasize that we do not attempt to explain the transition from foraging to agriculture here, rather we develop a model in which such a transition is feasible (i.e. not enforced or excluded a priori), and then explore whether such a transition could result in megafauna collapse.

Following Smith (1975), per capita food intake is defined as  $F = m + \mu p$ , where  $\mu$  is a plant-consumption parameter.<sup>5</sup> We assume households maximize a utility function,  $U$ , which is a function of food consumption and also a set of other goods like clothes, tools, and shelter, denoted  $v$ .<sup>6</sup> Utility is defined as

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<sup>5</sup> The assumption of perfect substitution between meat and produce is convenient but strong, and effectively rules out that meat becomes a valued luxury good when megafauna runs out.

<sup>6</sup> By assuming Paleolithic households maximize a conventional utility function we follow the standard neo-classical perspective, a restrictive presumption given the accumulated experimental evidence on behavioral anomalies (see for example McFadden 1999, Kahneman and Tversky 2000). We recognize and appreciate that people have values beyond the typical narrow definition of rationality. We also are aware rational choice is less likely to hold up when people make decisions outside the perimeters of an active exchange institution that rewards consistent and punishes inconsistent choices (Cherry et al., 2003; Smith, 2003). In effect, our model creates a “rational early man” benchmark that serves to expand the paleontology literature that generally assumes away economic tradeoffs—an extreme and unsatisfying simplification of actual human choice. This benchmark behavior rests on evidence that suggests early humans were not all that different from us today (e.g., Diamond). They knew art and culture, created exchange institutions to trade goods over long distances, and consumed and produced a variety of goods (Tattersall and Schwartz 2000). The evidence suggests early human behavior was more complex than that of animals and that consistent choices that maximized net rewards could have been reinforced by early institutional and social norms. In his book aptly titled “Thoughtful Foragers”, Mithen (1990) demonstrates that economic models can be applied to understand better prehistoric decision-making. Also see the work by Smith (1975) and Nerlove (1993), and the work on natural resource use by “primitive” cultures, such as Brander and Taylor’s (1998) study of Easter Island. That said, an interesting



$$(1) \quad U = (m + \mu p)^\beta v^{1-\beta},$$

which may be considered a hybrid form of Smith (1975) and Brander and Taylor (1998).

Households maximize (1) subject to a time constraint:

$$(2) \quad l = e + a + y,$$

where  $l$  is the total labor endowment,  $e$  is hunting effort,  $a$  is effort devoted to agriculture (or gathering), and  $y$  measures effort to produce other goods. The underlying assumption is that primitive hunters solve a series of static labor allocation problems rather than a single dynamic optimization problem. This presumption is consistent with observations by Mithen (p.224): “hunter-gatherers do not appear to plan subsistence activities over time scales longer than one year.” Our assumption is also consistent with more contemporary instances of open access resource exploitation (see Sanchirico and Wilen 1999; Bulte and Horan 2003). We abstract away from spatial considerations<sup>7</sup> and also ignore any institutional change that might arise in response to changes in resource scarcity (see Ostrom 1990, Erickson and Gowdy 2000, Pezzey and Anderies 2003).<sup>8</sup>

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avenue for future research is to consider the consequences of assuming a proportion of the early human population exhibits non-neo-classical preferences such as loss aversion, ambiguity aversion, time-inconsistency, and context-dependent preferences. Against our rational benchmark, one can then explore the power of instinct versus choice and heuristics versus optimization on patterns of early human development.

<sup>7</sup> Early overkill models attempted to capture spatial considerations to a certain extent (Mosimann and Martin 1975, Whittington and Dyke 1984). They were based on the hypothesis of an *advancing front* of humans, radially migrating Southwards and “locking up” animals in an increasingly small range. After local extinction of the megafauna, the front jumped forward, abandoning previous hunting grounds and reducing the available range for wildlife, as animals are prevented from “leaking” into unoccupied territory behind the front. However, the fossil evidence does not provide support for an advancing front moving south (Beck 1996). A front may not materialize because of coordination costs associated with moving many people or because of geographical barriers (mountains, deserts) that prevent the formation of a closed front. For these reasons we apply a non-spatial model and leave spatial concerns for future research. Alroy (p.1895) also argues “geographical dispersal is not a key factor.”

<sup>8</sup> We recognize the limits in presuming labor flows freely from one activity to another in response to differences in return to effort. This modeling assumption discounts the possible ‘frictions’ caused by traditions, customs, and ‘myths,’ and therefore represents one extreme. The opposite extreme exists if people did not actively allocate labor among hunting and farming, but rather maintained a single profession. A convenient way to capture this alternative scenario is to model two separate human populations that do not intermix, farmers and hunters. On the hunting side, this is essentially the “no agriculture” model we explore below. Since we assume early farmers do not compete, directly or indirectly, for wildlife resources, the dynamics of the society of proto agriculturalists has no impact on the megafauna population. The dynamics of interest (hunters and wildlife) are explored in the “no agriculture” model below.

Next consider human and megafauna dynamics. Human-megafauna dynamics are based on a modified form of a conventional predator-prey model (e.g., Lotka and Volterra). Such models have been used to examine human-wildlife interactions in other contexts (e.g., Brander and Taylor), but unlike Brander and Taylor, we distinguish between wildlife and plant food sources. Human population growth (fertility) depends on the available food supply, particularly for people living close to subsistence (see Dasgupta 1995; Nerlove 1991, 1993; Frisch 1978). Let the dynamics of the human population be

$$(3) \quad N_{t+1} - N_t = g(N_t, F_t),$$

where  $g(N, F)$  is the population growth function that combines both natural mortality and reproduction processes. The population growth function is

$$(4) \quad g(N_t, F_t) = rN_t \left(1 - \frac{S}{F_t}\right) = rN_t \left(1 - \frac{S}{m_t + \mu p_t}\right),$$

where  $r$ , the maximum potential growth rate, also measures the sensitivity of the human population (measured in households) to changes in nutrition (measured in calories).  $S$  is a fixed subsistence level. Population growth is positive ( $g > 0$ ) when  $F > S$ , negative ( $g < 0$ ) when  $F < S$ , and zero when  $F = S$ . The specification in (4) is analogous to existing non-instantaneous adjustment processes such as conventional open access fishery models in which it is commonly assumed profits drive entry and exit in the fishery sector, when profits are positive (i.e., whenever nutrition levels are in excess of the benchmark  $S$ ), aggregate effort in harvesting increases (e.g., Smith 1968, 1969).<sup>9</sup> The specification in (4) enables us to

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<sup>9</sup> This specification of population growth is Malthusian in spirit; it presumes caloric intake governs the dynamics, eventually restricting the system to steady states (if they exist) where survival is at the subsistence level. The specification does not address population control, which is a limitation given evidence that contemporary foraging societies make efforts to control fertility. Marceau and Myers argue that Paleolithic people too controlled their populations and suggest that various methods population control may have been used including “culturally-demanded abstinence, disruption of the menstrual cycle through extended breast feeding, abortion, direct and indirect infanticide (particularly female infanticide) and even dietary cannibalism.” Examining the consequences of fertility choice is an interesting extension of our model, and one we leave for future work. Such socially coordinated choices suggest a certain level of planning, cooperation and foresight, features not addressed in our model.

vary the fertility rate across societies to accommodate the evidence that a sedentary lifestyle that comes with proto agriculture may increase female body fat and thus fertility.<sup>10</sup>

Now consider the ecological side of the model. Following Mosimann and Martin, Smith, Brander and Taylor and others who have looked at resource extraction in a “simple economy,” we combine different megafauna populations into a single aggregate variable  $x$  and assume aggregate replenishment is described by a logistic growth function,  $G(x)=\alpha x(1-x/k)$ , where  $\alpha$  is the intrinsic growth rate and  $k$  is the carrying capacity. Megafauna population growth is reduced by human harvests, so the dynamics of the megafauna stock are described by the following difference equation:

$$(5) \quad x_{t+1} - x_t = \alpha x_t \left(1 - \frac{x_t}{k}\right) - N_t m_t.$$

We now return to the utility maximization problem defined by expressions (1) and (2). Assuming constant returns to scale to produce other goods, we choose units such that  $v = y$ . Harvesting of plants is represented by the function  $p = a^\eta$ , with  $0 < \eta \leq 1$ . Finally, harvesting of meat is defined by the standard Schaefer production function (Clark 1990):

$$(6) \quad m = qex,$$

where  $x$  measures the extant population (i.e., biomass) of megafauna.<sup>11</sup>

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<sup>10</sup> A referee correctly points out that subsistence levels may differ between hunters and agriculturalists due to the different caloric requirements associated with each activity, and growth rates would differ across activities. We capture this by the parameter  $\mu$  in (4). Let  $S$  be the subsistence level associated with hunting and let  $S'$  be the subsistence level associated with agriculture. The growth function  $g=rN(1-S/[m+(S/S')\mu p])$  captures the effect of differential subsistence rates: for instance, if  $m=0$ , then  $g= rN(1-S'/[\mu p])$  so that growth only depends on agricultural subsistence; if  $p=0$ , then  $g=rN(1-S/m)$ , and only  $S$  matters. This new specification is analytically equivalent to (4) if we replace  $\mu$  in (4) with  $\mu' = (S/S')\mu$ . It is unknown whether  $S$  is larger or smaller than  $S'$ , at least for the time period in question. We know agriculture is a more sedentary activity that may enhance the storage of body fat, which promotes fertility. The transition to agriculture eventually translated in massive growth of human populations (e.g. Diamond 1992). However evidence exists that people were less nourished (e.g., they became shorter and did not live as long) and less fertile *immediately* after the transition to agriculture (e.g. Angel 1975, Haviland 1993, Megarry 1995). The net effect is unclear. As a robustness analysis we explore what happens when subsistence requirements differ across activities. For our numerical results, our base case involves  $S=S'$ , so that  $\mu' = \mu$ . We also consider an alternative specification in which  $\mu$  increases by 33.3 percent, which is analytically the same as increasing  $\mu'$  by 33.3 percent while holding  $\mu$  constant, so  $S>S'$ . This alternative scenario models agriculture as more sedentary, requiring fewer calories and resulting in increased population growth rates.

Substituting the three production relations into (1), the Lagrangean associated with the hunter's problem is

$$(7) \quad L = (qxe + \mu a^\eta)^\beta y^{1-\beta} + \lambda[l - e - a - y].$$

We examine the solution to this problem by focusing on several special cases leading up to the general case defined in expression (7). We consider three possible combinations of parameters and discuss whether megafauna collapse is likely to occur. We resolve the many ambiguities that arise by using numerical simulations of key examples.

### 2.1. Case I: No plant consumption ( $\mu=0$ ).

First, consider the case in which the plant-consumption parameter is zero,  $\mu=0$ , the case considered by Mosimann and Martin who argue early humans ate mostly meat. The opportunity cost of hunting in terms of foregone agricultural products (what Smith refers to as the wage rate in agriculture) is defined as  $\mu/q$ . With  $\mu=0$ , this wage rate is zero because megafauna are the only food source. In a model with no human population growth, Smith (1975) finds that megafauna extinction might result if the wage rate in agriculture is small enough so that a sufficiently large share of labor is allocated to hunting. The smallest possible wage rate in agriculture is zero, the present case.

The optimal solution to expression (7) when  $\mu=0$  is  $e^*=\beta l$ , so that  $m^* = q\beta l x$  and  $a^*=0$ . The model is fully described by the difference equations (4) and (5) and, assuming an interior steady state exists, we find this steady state by setting  $N_{t+1} = N_t$  and  $x_{t+1} = x_t$ :

$$(8) \quad N^* = \frac{1}{q\beta l} \left( \left[ k - \frac{S}{q\beta l} \right] \frac{\alpha}{k} \right).$$

$$(9) \quad x^* = \frac{S}{q\beta l}.$$

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<sup>11</sup> A more general specification, albeit analytically less tractable, is the specification  $m = qex^\phi$  and  $\phi < 1$  (e.g. Henderson and Tugwell 1979). Our main empirical results are qualitatively robust for this extension.

We examine the stability properties of this equilibrium in an Appendix available on the JEBO website and in the numerical analysis in section 2.4 and show that extinction is unlikely (also see Clark 1973).<sup>12</sup>

Given Smith's finding that extinction only occurs under a small agricultural wage rate, our results might seem to suggest that the presence of agriculture could not have caused the megafauna extinction, but that is not necessarily true. The plausible combination of agriculture and endogenous human population growth could have done the trick, a case to which we now turn.

## 2.2. Case II: Positive plant consumption and CRTS in agriculture ( $\mu > 0$ , $\eta = 1$ )

Suppose now that agriculture/gathering represents an alternative food source ( $\mu > 0$ ), resulting in a positive agricultural wage rate.<sup>13</sup> If constant returns to scale in agriculture exist ( $\eta = 1$ ), the solution to (7) is  $e^* = \beta l$ , so that  $m^* = q\beta l x$  and  $a^* = p^* = 0$  whenever  $x > \mu/q$ , and  $a^* = \beta l$ , so that  $p^* = \beta l$  and  $e^* = m^* = 0$  whenever  $x < \mu/q$ . As megafauna become scarce, all hunting activity ceases as everyone switches entirely to agriculture/gathering. Due to the linearities in production and consumption (preferences), complete specialization occurs in response to small differentials in returns to labor effort. Accordingly, a constant amount of effort,  $\beta l$ , will be devoted to the specialized activity (with  $[1 - \beta]l$  devoted to production of  $v$ ).

Because hunting and agriculture are not undertaken simultaneously, the steady state equilibrium of  $x^* = S/(q\beta l)$  (as defined by (9) for the case of no agriculture) will arise if  $S/(q\beta l) > \mu/q$ . For  $x > x^*$ , people specialize in hunting, the human population grows, and

<sup>12</sup> This result may not be surprising since megafauna extinction would cause human extinction given endogenous human population growth based on a single food source, but extinction is not ruled out *a priori* by the combination of logistic growth and Schaefer production. In continuous time, the slope of dynamic trajectories go to infinity as the stock approaches zero, but this does not carry over to the context of discrete time. Harvesting success is determined by effort and the wildlife stock *at the beginning* of the period, which implies that the stock can well be drawn down at finite cost. Overshooting can occur during the approach dynamics, triggering system collapse, much as extinction can occur in an open access fishery when exit is slow in response to negative profits (e.g., Bjorndal and Conrad 1987).

aggregate harvests increase as the stock is depleted towards  $x^*$ . For  $\mu/q < x < x^*$ , people specialize in hunting but the human population falls. Aggregate harvests fall and the stock increases towards  $x^*$ . For  $x < \mu/q < x^*$ , agricultural specialization occurs, allowing the stock to recover. Moreover, food production under agricultural specialization,  $\mu\beta l$ , is not sustainable ( $\mu\beta l < S$ ), food consumption would be at a level below subsistence requirements and the human population would fall until hunting again became profitable. The only possible equilibrium is the same that arises when people eat only meat ( $\mu=0$ ): agricultural food (gathered product) is too expensive and people sustain themselves by eating only meat in the steady state. Here megafauna are even less likely to go extinct due to overshooting than they were in the case of no agriculture ( $\mu=0$ ). If megafauna became sufficiently scarce (i.e.,  $x < \mu/q$ ) along the transition to the steady state  $x^*$ , people would temporarily switch to agriculture/gathering during this transition phase. This would allow the stock to recover as opposed to driving it to extinction, while at the same time reducing the human population and thereby easing the aggregate hunting pressure that arises when hunting again becomes profitable.

If  $S/(q\beta l) < \mu/q$ , then  $S < \mu\beta l$ , which implies that engaging exclusively in agriculture/gathering is sustainable. A steady state equilibrium involving a positive megafauna stock does not emerge in this case. As the megafauna stock is depleted below  $\mu/q$ , meat becomes too expensive and everyone switches to agriculture/gathering, but this is only temporary as the stock recovers and the catch per unit of effort increases. Pulse harvesting would be optimal around the point  $x = \mu/q$ . Moreover, the size of the aggregate pulse harvest increases over time due to an expanding human population. When  $x > \mu/q$ , all effort goes into hunting and the human population grows since  $x$  is larger than the stock that

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<sup>13</sup> For simplicity, we do not address the effect of expanding agriculture on the size of natural habitat available for wildlife.

would yield subsistence harvests (i.e.,  $x > S/(q\beta I)$ ). As  $x$  falls below  $\mu/q$ , the human population expands when everyone switches to agriculture/gathering. The human population is in a continuous state of growth, even when hunting again becomes profitable, but with profitable hunting, the larger population results in ever-greater waves of harvesting pressure. In the limit as  $N$  grows, a single pulse harvest could cause extinction.

This result arising from endogenous human population growth contrasts with Smith's (1975) findings in two key ways. First, we find megafauna extinction might occur when the agricultural wage rate is *large*, rather than *small*. Second, we find increased population pressure as a result of diversifying into agriculture causes extinction, even under constant returns to scale. In contrast, Smith (1975, p. 741) states "With constant returns in agriculture, equilibrium requires total hunting intensity to be constant...once a hunting society diversifies into agriculture (or gathering), the presence of increasing population pressure on animal stocks disappears." We address later whether this is likely to have happened in reality.

### 2.3. Case III: Positive plant consumption and DRTS in agriculture ( $\mu > 0$ , $\eta < 1$ )

The assumption of constant returns to scale in labor seems too strong since other inputs such as seeds and tools (and even weather) represent limiting factors. Consider what happens when agriculture/gathering is characterized by diminishing returns to labor (i.e.,  $\eta < 1$ ). As we found before, increased scarcity of megafauna results in a reallocation of labor from hunting into agriculture, although now hunting does not totally cease for some positive megafauna stock levels. Instead, optimal labor allocations to agricultural/gathering and hunting are

$$(10) \quad a^* = \left( \frac{\mu\eta}{qx} \right)^{\frac{1}{1-\eta}}, \text{ and}$$

$$(11) \quad e^* = \beta l - \left( \frac{\mu \eta}{qx} \right)^{\frac{1}{1-\eta}} \left( \frac{1 - \beta + \beta \eta}{\eta} \right).$$

From expression (10), we see that positive levels of effort are always applied towards agricultural/gathering endeavors (except for the limiting case as  $x \rightarrow \infty$ ). In contrast, equation (11) indicates that harvesting ceases when the megafauna stock falls below a value

of  $\hat{x} = \frac{\mu \eta}{q} \left( \frac{\beta \eta}{1 - \beta + \beta \eta} L \right)^{\eta-1}$ . When  $\eta=1$ , this threshold reduces to  $\mu/q$  as before. In an

interior equilibrium, it must be that  $x^* > \hat{x}$ , where the steady state wildlife stock,  $x^*$ , is derived from (10) and (11) and therefore differs from equation (9).

We can use the optimal labor allocations defined by (10) and (11) to solve for interior steady state values  $x^*$  and  $N^*$ . This solution must be obtained numerically, however, because nonlinearities prevent the derivation of an explicit analytic solution. Accordingly, the stability properties must also be derived numerically. If the equilibrium is stable, extinction may not be a concern. Whether equilibrium is stable, however, is ambiguous due to two competing effects, a labor allocation effect and a population growth effect.

Unlike the outcome when  $\mu=0$ , now labor is allocated to both hunting and agriculture for the present interior steady state. If other things were held equal, this implies a reduction in per capita harvesting relative to the case in which  $\mu=0$ , making extinction less likely. But other things are not held equal because the size of the human population is different. With a larger population, overall hunting effort may increase even though per capita hunting effort is decreased. The net impact on megafauna populations is ambiguous. Smith (1975) also notes that population pressure could be an issue in the presence of decreasing returns to scale in agriculture.



## 2.4. Empirical application of the theory

We calibrate the empirical model using data for North America. The following parameter values represent the ‘best-guesses’ available from the literature (see Appendix A for derivations):  $S = 2.9\text{AU}$  (animal units, where 1 AU equals 1,000 pounds of living animal),  $q = 8.3 \times 10^{-11}$ ,  $r = 0.0443$ ,  $\beta = 0.6$ ,  $l = 7300$ ,  $k = 75$  million AU, and  $\alpha = 0.1$ ,  $\eta = 0.45$ , and  $\mu = 0.045$ .<sup>14</sup> These parameter values, which imply the case of diminishing returns to labor in agriculture (or Case III above), represent our benchmark scenario in what follows. As discussed in Appendix A, agricultural productivity in this model is probably at greater levels than would have occurred under European agriculture during this time period and also greater than gathering productivity in North America. We show in what follows, however, that agriculture probably had little impact on megafauna extinction even under these biased conditions. Moreover, land area also has little impact on the results. This suggests that the results for North America could apply to Europe too.

Figure 1 and Table 1 present the results of the benchmark simulations. Figure 1 illustrates the first 1,000 years of the simulation, a time interval consistent with the usual predicted interval until megafaunal extinction (see Mosimann and Martin). The system converges upon a steady state within the first 400 years. This result suggests that neither endogenous human expansion nor agriculture/gathering as alternative food options results in megafaunal collapse. Rather predator and prey co-exist at intermediate densities. Figure 1 illustrates that a boom-and-bust pattern occurs initially (see Brander and Taylor for a similar result), followed by stabilization of both populations.<sup>15</sup> This result can be compared with the case of no agriculture in Figure 2. Without agriculture, many boom and bust cycles emerge

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<sup>14</sup> An animal unit is the equivalent of 1,000 pounds of living animal; one fully grown *Mammuthus imperator* may equal more than 20 AUs, but for most species there are considerably fewer AUs per animal.

<sup>15</sup> Although Nerlove (1993) has endogenous population growth, subsistence is not accounted for, so his model would not predict such a boom-and-bust pattern.

and stabilization does not occur within the 1000-year interval (it takes another 600 years to occur). Agriculture has a stabilizing effect.

Table 1 summarizes the key results from the benchmark model, the alternative scenarios involving agriculture, and our sensitivity analysis. In the benchmark case, the majority of time is spent in hunting, with little time in agriculture. No time is spent in agriculture in the two alternative agricultural scenarios (No Agriculture [ $\mu=0$ ] and Constant Returns to Scale Agriculture [ $\eta=1$ , with  $\mu=0.0055$  for this case since  $\eta$  is used to calibrate  $\mu$ ; see Appendix A])). Comparison of these scenarios with the baseline case illustrates the impact of agriculture on megafauna stocks and the human population. Agriculture results in megafauna stocks diminished by 9 percent and the human population increased by 25 percent. Even with a significantly larger human population, the impact on megafauna stocks is small.

For the sensitivity analysis, we test the robustness of megafaunal survival by biasing the key parameters toward overkill. We increase the parameters  $\beta$ ,  $q$ ,  $r$ ,  $\mu$ , and  $l$  by  $1/3$ , and decrease the parameters  $S$ ,  $\alpha$ , and  $k$  by  $1/3$  to enhance the probability of overkill.<sup>16</sup> We find the robustness checks are consistent with intuition. Our main result is robust with respect to key variables, and the model consistently predicts megafaunal survival rather than collapse. The parameter having the biggest impact on megafauna stocks is the caloric requirements for human survival,  $S$ . Megafauna stocks are diminished substantially in this case due to a larger human population. An offsetting effect is that people spend more time in agriculture and much less time in hunting the now relatively scarce megafauna.

As mentioned, we may re-interpret the no-agriculture case ( $\mu=0$ ) as the special case where humans are subdivided in hunters and farmers (i.e. infinitely slow reallocation of labor

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<sup>16</sup> As we discuss in footnote 10, increasing  $\mu$  is akin to decreasing the subsistence requirements for agriculture relative to hunting. Even with substantially lower subsistence requirements for agriculture, which from Table 1

in response to arbitrage opportunities). Since we find, numerically, that both extreme behavioral benchmarks (i.e., instantaneous adjustment and no adjustment) result in megafauna survival, we believe it is likely that similar outcomes emerge in models with assumptions based on "intermediate" labor mobility.

## 2.5 Extensions: CES utility and critical depensation

We now explore whether our human-megafauna co-existence result is robust to two alternative functional specifications: differences in the elasticity of substitution and critical depensation in megafauna growth. First, we replace the Cobb-Douglas utility with CES utility in which the elasticity of substitution between food and other goods in the utility function,  $\sigma$ , is not unity.<sup>17</sup> Define  $U=(m^\beta+v^\beta)^{1/\beta}$ . The only plausible case is when meat and other goods are net complements,  $\sigma<1$ .<sup>18</sup> Re-running the model, we find our key results are robust. Even if we consider the extreme case in which all households spend all their time hunting (i.e.,  $\beta=1$ ), the system converges to a stable interior solution of around 5 mln AUs (after reaching an all-time low of 1.6 mln AU after 225 years).

Second, we augment the growth function by the classic minimum viable population (MVP) concept. For the growth function to display critical depensation, we add a shift parameter, a constant  $Q$ , so the function intersects the horizontal axis at stock levels lower than before but still somewhat greater than zero (and smaller than  $K$ ). Assume that 10,000 animal units (AU) is a reasonable estimate for the MVP (see Primack 1998).<sup>19</sup> While the

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indicate a 33.3 percent increase in the human population, we find megafauna do not go extinct. The reason is an endogenous reallocation from time spent hunting to time spent in agriculture.

<sup>17</sup> The unity restriction implies households spend a constant proportion of their time hunting ( $\beta$ ), no matter how hungry they are, an unrealistic abstraction.

<sup>18</sup> If  $\sigma>1$ , meat and other goods are net substitutes, which is implausible. This would mean households hunt less as the megafauna stock declines and choose to go hungry while increasing their consumption of other goods. Households spend more time hunting as the prey base grows scarce to maintain reasonable food intake. The optimal allocation of time between the two activities is defined by  $e^*=l/(1+q^\beta x^\beta)$ , such that  $e \rightarrow l$  as  $x \rightarrow 0$ .

<sup>19</sup> Depending on the species, this amounts to hundreds or thousands of individual animals. While this may seem large in relation to MVP estimates commonly found in the conservation literature, recall we are considering megafauna, or multiple species (such that breeding success is lower than when considering a single species, i.e.,

resulting equilibrium is affected by the introduction of critical depensation (e.g.  $x^* = 7,977,114$  AU and  $N^* = 245,472$  for the case without agriculture), the qualitative results are again not affected by this extension.

### 3. Another Alternative Food Source: Small Animals as Outside Options

These results suggest that agriculture is unlikely to lead to human overkill, but does this weaken the case for overkill as the cause of megafauna extinction? Not necessarily. What if there was another food source that had the effect of directly encouraging overkill? Consider the impact of small prey, or ‘minifauna’. Many observers argue it is likely that Pleistocene hunters also killed smaller prey such as deer and hares. Stiner (1992), for instance, concluded that European hominids preyed on 28 species in the Middle Paleolithic hominids and 15 species in the Late Upper Paleolithic. Prey ranged from pachyderms to small ungulates, reptiles, and birds.

Earlier simulation studies, however, have not addressed how small animals affect the primitive hunter’s opportunity set. Rather, previous work has restricted the hypothetical prey to those species of large mammals that became extinct, perhaps because the fate of these charismatic species was considered most interesting. Smith (1975) mentions how early humans may have switched to “supplemental game” as megafauna became extinct, but since his model includes neither human population dynamics nor multiple species populations, he

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not all males can team up with all females now). Including an MVP of 10,000 AUs with negative (positive) growth of the megafauna population whenever  $x < (>) 10,000$  implies we rewrite the growth function as  $G(x) = \alpha x(1 - x/k) - F(x=10,000) = \alpha x(1 - x/k) - Q$ . Megafauna population growth is reduced by human harvests, so the dynamics of the megafauna stock are described by the difference equation:

$$(5') \quad x_{t+1} - x_t = \alpha x_t \left(1 - \frac{x_t}{k}\right) - 10,000\alpha \left(1 - \frac{10,000}{k}\right) - N_t q \beta l x_t.$$

As a consequence, we rewrite the  $\Delta x = 0$  isocline:

$$(8') \quad N^* = \frac{1}{q\beta} \left( \left[ k - \frac{S}{q\beta} \right] \frac{\alpha}{k} \right) - \frac{Q}{S}.$$

does not consider the issue in detail. We argue and our results support the idea that small animals might be more important to understanding the fate of large animals than previously appreciated.

We now add small animals as substitute prey into our model (which is essentially analogous to analyzing a multi-species fishery rather than a single species fishery, e.g., Clark 1990, 311-13). Assume megafauna and minifauna are ecologically independent, no interaction through the growth functions, and both are jointly subject to hunting effort by early humans.<sup>20</sup> Initially, assume humans do not discriminate hunting effort between large and small species; they decide about the optimal level of aggregate effort, as before. In effect, this is the opposite case of gathering considered in section 2: as the megafauna population falls there is no transfer of effort from mega- to minifauna, which is a stylized extreme case in this context (but see below). Define the harvesting of large and small animals by the respective production functions. This is consistent with observations by Mithen, who argues that the predominant mode of hunting was on an *encounter basis*. Denoting biomass (measured in AUs) of small prey as  $z$ , total meat production is defined as

$$(12) \quad m = e[qx + q'z],$$

where  $q'$  is the *catchability coefficient* of small prey. Define the dynamics of small prey as:

$$(13) \quad z_{t+1} - z_t = \gamma z_t \left(1 - \frac{z_t}{h}\right) - N_t q' e z_t,$$

where  $\gamma$  is the intrinsic growth rate of small prey, and  $h$  is the carrying capacity for such animals. Small prey replenishes much faster than megafauna and are more difficult to catch. In addition many large species tended to congregate in herds, making them relatively easy to detect and harvest (Smith 1975). Assume the catchability coefficient is less for small animals

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The revised isocline is non-monotone in the prey stock  $x$ : it is upward sloping ( $dN/dx > 0$ ) for  $x < \sqrt{Qk/\alpha}$  (and approaches minus infinity as  $x$  goes to zero), and downward sloping for  $x > \sqrt{Qk/\alpha}$ . Using the empirical data mentioned above, the  $dx/dt=0$  isocline peaks at  $x=866,025$  AUs.

relative to larger species,  $q' \leq q$ .<sup>21</sup> Hence  $\alpha/q < \gamma/q'$ , where the ratio of a species' intrinsic growth rate to its catchability coefficient measures a species' *biotechnical productivity* (see Clark 1990, 315).

From expressions (5) and (13) (given that aggregate megafauna harvests are still  $qex$ ), an interior equilibrium solution ( $x_{t+1} = x_t = x > 0$ , and  $z_{t+1} = z_t = z > 0$ ) only exists for points  $(x, z)$  on the line segment:

$$(14) \quad \frac{\alpha}{q} \left(1 - \frac{x}{k}\right) = \frac{\gamma}{q'} \left(1 - \frac{z}{h}\right),$$

where  $0 < x \leq k$ , and  $0 < z \leq h$ . Rewrite this condition as

$$(15) \quad z = h \left(1 - \frac{\alpha q'}{\gamma q}\right) + \frac{\alpha q' h}{\gamma q k} x.$$

The first term on the right-hand-side of expression (15) is positive, as is the coefficient of  $x$ .

Thus,  $z$  is positive for very small values of  $x$  and is increasing in  $x$ .

For an interior equilibrium solution, the human population should also be constant ( $N_{t+1} = N_t = N > 0$ ), hence  $S=F$ . Consider the case of diminishing returns to labor in agriculture ( $\eta < 1$ ), here effort may be involved in both hunting and agriculture. In this case, we derive the following condition from the subsistence equilibrium condition  $S=F$  and from conditions (4) and (10)-(12):

$$(16) \quad S = \left[ \beta l - \left( \frac{\mu \eta}{qx} \right)^{\frac{1}{1-\eta}} \left( \frac{1 - \beta + \beta \eta}{\eta} \right) \right] (qx + q'z) + \mu (\mu \eta)^{\frac{\eta}{1-\eta}} (qx + q'z)^{\frac{-\eta}{1-\eta}}.$$

Define  $\xi = qx + q'z$ . Equation (16) is a polynomial in the variable  $\xi$ . If an interior solution exists in the case of no minifauna ( $z=0$ , as in section 2), at least one real, positive root of (16)

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<sup>20</sup> If we assumed megafauna competed for forage with small animals, our results would be further supported as a diminishing megafauna stock would lead to larger growth of minifauna.

<sup>21</sup> It may be easier for individual households to harvest small prey than to target giants like mammoths or mastodons, but when hunting takes place in dispersed small groups, large prey may be targeted, especially when harvesting is facilitated by the usage of tools such as javelins and arrows (see McDonald 1984). Large mammals may also be caught in pits dug across habitual trails.

exists, denoted  $\xi^* > 0$  (there may be several). Given this solution, condition (16) can be rewritten as

$$(17) \quad z = \frac{1}{q'} \xi^* - \frac{q}{q'} x.$$

The equilibrium conditions (15) and (17) can be plotted in a  $z$ - $x$  phase plane. Drawing small prey  $z$  on the vertical axis and megafauna  $x$  on the horizontal axis, condition (15) is an upward sloping line segment and condition (17) is a downward sloping line segment, both with positive vertical intercepts.

We now define the condition to determine megafauna survival or extinction given small animals. An interior equilibrium exists for megafauna survival if and only if the two line segments cross, and this only happens if the intercept in equation (17) is greater than the intercept in equation (15), that is if

$$(18) \quad \phi = \frac{1}{q'} \xi^* - h(1 - \frac{\alpha q'}{\gamma q}) > 0.$$

If (18) holds ( $\phi > 0$ ), a unique interior solution exists and may be found by solving expressions (13), (15) and (16). If the reverse inequality holds ( $\phi < 0$ ), an interior solution does not exist and the megafauna population (with low biotechnical productivity) is driven to extinction by the expanding human population feeding mainly on small prey.

### 3.1. Empirical application of the theory

We now parameterize our model for small animals,  $z$ , to determine whether condition (18) holds. Assume the maximum density of suitable small prey per square mile is 10 AU, such that  $h = 30$  million (see Appendix A). Also assume an intrinsic growth rate  $\gamma = 0.4$  (Mosimann and Martin), and for lack of better information, initially assume  $q' = q$ .

Table 2 presents the results of the benchmark case, the alternative agricultural scenarios, and a sensitivity analysis (in which parameters are increased or decreased by 1/3 to

bias the outcomes against overkill). We find that megafauna go extinct in every case. This is our key result, an interior solution does not exist for this dynamic system, which implies megafaunal collapse. Moreover, comparison of the benchmark case with the agricultural scenarios illustrates that agriculture had nothing to do with the megafauna extinction. Instead, small animals matter to megafauna extinction. Primitive man hunts megafauna to extinction because the rapidly replenishing population of minifauna continues to support the human population even as the megafauna stock collapses.<sup>22</sup> Figure 3 illustrates the gradual substitution of minifauna for megafauna in the human diet. As a point of comparison, megafauna collapse is avoided whenever the growth rate of megafauna ( $\alpha$ ) exceeds 31% (given all other benchmark parameters), which is unrealistic given that the intrinsic growth rate of contemporary megafauna as elephants and rhinos is only 7% and 16% (Milner-Gulland and Leader-Williams 1992).

Why is agriculture not a factor? The reason is that agriculture and hunting are *substitute* activities for labor. Spending more time in agriculture means spending less time hunting. The only way that agriculture can lead to megafauna collapse is through the larger population that agriculture can support, but we find this population enhancement effect is dominated by the labor substitution effect. In contrast, hunting large and small prey are *complementary* activities. Spending more time hunting means that chance encounters with megafauna are more likely, even when megafauna are scarce. These encounters are further supported by the large human population that minifauna are able to support while megafauna are diminished.

The conclusion that prey substitution matters is consistent with observations on contemporary extinctions caused by the brown tree snake, *Boiga irregularis*, an invasive species causing both ecological and economic damage on Guam since the 1960s (Savidge,

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<sup>22</sup> As megafauna become extinct, there is a downward adjustment of the human population. While substituting



1987).<sup>23</sup> The brown tree snake threatens the majority of forest avifauna on Guam because it preys on many species (e.g., lizards, rodents, birds). Consistent with the outcomes of our model albeit in a different context, Savidge (p.667) notes “[s]mall lizards are exceedingly common on Guam, and apparently their reproductive potential is high enough to withstand the predation pressure... By utilizing this abundant lizard prey resource, *Boiga* can maintain high densities while decimating its more vulnerable prey (birds).” Replace “small lizard” in this passage with “minifauna” and “birds” with “mammoths,” and the story is analogous to ours.

### 3.2. Extension: separate effort for minifauna and megafauna

Finally, we consider what might happen if hunters applied differentiated techniques for hunting megafauna and minifauna. We distinguish between two cases. First, hunters distinguish between megafauna and minifauna meat ( $m_1$  and  $m_2$ ), and allocate effort ( $e_1$  and  $e_2$ ) to target each types selectively.<sup>24</sup> We have  $U = m_1^\beta m_2^\omega v^{1-\beta-\omega}$ ,  $l = e_1 + e_2 + a$ ,  $m_1 = q_1 e_1 x$  and  $m_2 = q_2 e_2 z$ . The optimal amount of megafauna hunting effort is defined as  $e_1^* = \beta l$ , which means that the qualitative results of the model remain robust to this specification. Second, suppose instead hunters discovered that differentiated hunting habits maximize total output. They tailor their techniques to the habitat or species habits to increase the probability they encounter the preferred type. We have  $U = m^\beta v^{1-\beta}$  and  $l = e_1 + e_2 + a$  as before, but now  $m = m_1(e_1, x) + m_2(e_2, z)$ . The functions  $m_i$ ,  $i=1,2$  represent meat output resulting from a certain allocation of “specialized” hunting effort  $e_i$ . Assume  $m_1(0, x) = m_1(e_1, 0) = 0$ .

We consider two situations. If hunting habits are extremely differentiated so any effort allocated to activity  $e_1$  ( $e_2$ ) rules out harvesting any species 2 (1), we can reject the overkill hypothesis. A differentiated hunting habit, for example, is when hunters hunt small

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to small prey, humans temporarily fail to meet subsistence requirements.

<sup>23</sup> Thanks to Lars Olson for pointing out this interesting example.

animals by day and large ones by night, or *vice versa*. These day/night hunters allocate effort away from targeting megafauna when this population grows scarce ( $e_1^* \rightarrow 0$  as  $x \rightarrow 0$ ), effectively allowing a recovery to more abundant levels.

In contrast, if hunting habits are imperfectly differentiated, overkill again is plausible, albeit at a reduced pace and intensity. Now hunting habits (e.g., choice of habitat, tools, time of day, etc.) are biased towards a certain species at the expense of reduced probability of encountering the other type (accidental encounters or “bonus killings” still occur).<sup>25</sup> We rewriting equation (3) as  $m = q_1 e_1 x + q_2 e_1 z + q_3 e_2 x + q_4 e_2 z$ , where  $q_1$  is the catchability coefficient of megafauna when targeted,  $q_2$  is the catchability coefficient of minifauna when megafauna is targeted; and  $q_3$  and  $q_4$  are similarly defined for minifauna. Here  $q_1 > q_3$  and  $q_4 > q_2$ , the catchability coefficient of a targeted species is greater than for the bonus species, but the main results of the model are unaffected.

## 5. Concluding discussion

This paper addresses a classic Pleistocene puzzle of megafauna extinction from a behavioral perspective. We ask whether early humans with their primitive hunting technology and limited opportunity sets could have wiped out massive herds of large mammals about 12,000 years ago, and if so, what economic forces might have led to such an outcome. We address these questions by combining two key elements of conventional renewable resource models: (1) open access resource management and entry and exit (i.e., birth and death) in response to profits (human nutrition), and (2) multispecies harvesting with differential biotechnical productivity. Our model and empirical results suggest that the fate of megafauna is best understood with explicit reference to small animals as substitute prey

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<sup>24</sup> We do not address agriculture for simplicity.

<sup>25</sup> This story is consistent with joint poaching of elephants and rhinos in Africa. Rhino poaching is effectively “supported” by killing the relatively more abundant elephants (Milner-Gulland and Leader-Williams). Without the flow of ivory generated by poaching, rhinos hunting itself is a loss-earning activity. While chasing elephants, one can encounter a rhino and take it as a bonus.

(e.g., deer and hares). Moreover, the results absolve agriculture, which had previously been implicated as the cause.

Minifauna have been overlooked in previous simulation models examining megafauna extinction, perhaps because they live today and are less charismatic. Interestingly, the few researchers looking at small prey reach an opposite conclusion. Webster (1981), for example, argued that prey switching would break up a massive killing front (essentially, a wave of hunters advancing across North America killing everything in its path; see Mosiman and Martin 1975, Whittington and Dyke 1984), which would not support the paleontology overkill hypothesis.

These findings suggest some common ground between opposing factions studying megafauna collapse. While a consensus appears to have emerged that implicates overkill, some researchers still believe that climate change was the principal cause of extinction. Our findings provide some middle ground between the two views. The results suggest the interaction of climate and harvesting might have played an important role in triggering the demise of megafauna. The reason why minifauna emerged as an important complementary activity in North America, and not more benign activities like large-scale gathering or agriculture, may be the harsh climatic conditions that prevailed in the late Pleistocene. The climate may have set the stage for humans to behave in a way that was detrimental for megafauna; the location of megafauna in relation to climate and the prevalence of agriculture is likely to be of special relevance.

Finally, our results suggest that abundant small prey is a necessary condition for humans to reach critical densities to drive megafauna to extinction. Early humans were successful predators in a naïve ecological system, and they could have quickly reached critical densities to wipe out major prey species, provided they had small animals as an outside option. In fact, we biased our model toward megafauna survival by ignoring

technical change or learning-by-doing and ignoring possible adverse effects of human habitat conversion (e.g., habitat burns) on megafauna's potential to replenish. Nonetheless, our results suggest human overkill should be considered a real possibility, suggesting the popular image of early man as a "noble savage" living in "harmony with nature" might need revision. Our empirical results also indicate that "aggregating" wildlife into a single variable can obscure important underlying behavioral responses to changes in species composition.

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## Appendix A: Parameters for the simulation models.

*Modeling megafauna:* The carrying capacity for megafauna is based on evidence on contemporary African megafauna. According to Mosimann and Martin, the maximum megafauna density will be 25 animal units (AU) per square mile which, given the available range in the late Pleistocene, translates into  $k=75$  AU. (Mosimann and Martin assume that the available range for herbivores in North America in the late Pleistocene was 3 million square miles; the rest of the land surface was not suitable, possibly covered with ice sheets.) 1 AU measures 1,000 pounds of living animal. Assume the intrinsic growth rate of megafauna is 10%, a number somewhat lower than the optimistic number reported by Mosimann and Martin (who employed a growth rate of 25%), but higher than estimates of the growth rate of modern elephants (close to 7%).

*Modeling human population and behavior:* We assume an initial population of 100 households. Following Whittington and Dyke (1984, p.454) who present “parameters based upon empirical evidence generally acceptable to archeologists and human ecologists” we assume  $r = 0.0443$ . We assume that a prehistoric working day for the representative household (man, woman and two children) consists of about 20 hours per day (7300 hours per year), and that meat is the predominant source of food so that  $\beta=0.8$ . Finally, Dasgupta (1993) estimates that active humans should consume 2000 calories (0.73 AU) per day to sustain themselves; hence for a household of four we compute that  $S=2.9$  AU per year.

*Modeling harvesting of megafauna:* Mosimann and Martin assume that a single full-time hunter supports an entire family and harvests 13 AU per year for a wildlife density of 25 AU per square mile (hence:  $x=75$  million). Assuming the standard Schaefer production function  $y=qex$ , and assuming that such a full-time hunter goes out for 10 hours a day, we find that  $q = 4.7 \times 10^{-11}$ . Next, according to Mosimann and Martin, if megafauna density falls to 5 AU per square mile (so that  $x=15$  million), it is assumed that the annual harvest is reduced to 6.5 AU. Again, solving for the catchability coefficient we find that  $q = 1.2 \times 10^{-10}$ . As a benchmark parameter in our simulations, we apply the average of these two parameters, or  $q = 8.3 \times 10^{-11}$ . When megafauna stocks are ‘thick’ and when the meat parameter  $\beta$  is ‘large,’ harvest may be considerably larger than the subsistence level. This does not need to imply, however, that harvest effort will be adjusted downwards. For example, Mithen (1990) and others have argued that harvesting in excess of own needs may signal prestige and trigger reciprocal favors within ancient hunter communities.

*Modeling proto agriculture.* The general form of agricultural/gathering production is  $p = \zeta a^\eta$ , where  $\zeta$  is a scale parameter. Hyami and Ruttan (1970) estimate the elasticity of agricultural production with respect to labor ( $\eta$ ) to be in the range 0.3 – 0.49. We use the value 0.45, which is roughly equivalent to their instrumental variables estimate. For the scale parameter  $\zeta$ , we use data on maize production among smallholders who use low-input technologies in Mozambique. Strasburg (1997) estimates 82 mandays (656 hours) are spent per hectare to grow 194 kg/ha (0.47 AU/ha) among some of the less productive farmers (even low-productivity farmers in today's LDCs are likely to be more productive than gatherers or farmers who practiced primitive forms of agriculture, if for nothing else than the better plant varieties that exist today). This implies  $p / A = 0.47 = (\zeta / A)(656 / A)^{0.45}$ , where  $A$  is total land in agriculture. Hence,  $\zeta = (0.47 / 656^\eta) A^{1-\eta}$ . Spending 656 hours/ha, a family working full time in agriculture (i.e.,  $a = \beta L$ ) could work on  $A = 6.68$  ha. Hence  $\zeta = 0.0725$ . We keep the value of  $A$  fixed, so our production function overestimates productivity whenever a family divides its time between hunting and agriculture/gathering. Note that the production function in the text is defined as  $p = a^\eta$ . This is because we have incorporated  $v$  into the nutritional parameter  $\mu$  to reduce notation. In fact,  $\mu = \zeta \psi$ , where  $\psi$  measures the caloric value of agricultural/gathered food relative to meat. Using USDA estimates of food consumption in the early 1900s (when diets consisted of fewer processed and 'junk' foods) (Gerritor and Bente 2002), we find that average meat consumption was 0.45 pounds/day and contributed to 499.8 of a person's calories/day, or 1106.9 calories/pound. Fruits and vegetables accounted for 2.33 pounds/day and contributed to 1598 calories/day, or 686.8 calories/pound. We adopt a value of  $\psi = 686.8 / 1106.9 = 0.62$ . Hence  $\mu = 0.045$ .

*The small prey model.* For small prey we extend the analogy with contemporary African nature reserves that is the basis of the assumption that  $k = 25$  AU per square mile. According to Pratt and Gwynne (1977) and Prins et al. (2000), a reasonable assumption for the carrying capacity for herbivores is approximately 4 ha/AU, or 64 AU per square mile. Allocating 25 AU to "megafauna," some 39 AU per square mile remains for smaller species. We assume that 25% of the additional species are considered as "prey" by early human hunters; hence the maximum density of substitute prey is about 10 AU per square mile. Hence  $h = 30 \times 10^6$ .

## Appendix B: Local Stability Properties of Open Access Steady State

To examine the local stability properties of our planar system, we follow the approach outlined and discussed in Nerlove (1993, Fig. 1) and Azariadis and de la Fuentes (1993, Fig. 6.6).<sup>26</sup> To determine stability properties, we look at three items associated with the Jacobian matrix of the planar system (evaluated at the steady state): (i) the determinant, denoted  $D$ , (ii) the trace, denoted  $T$ , and (iii) the discriminant, denoted  $\delta$ . Note that analyzing the local stability properties of the multi-prey model *after* extinction of megafauna is exactly analogous to examining the properties of the megafauna model: the planar system involves a single predator (humans) and a single prey population (megafauna or minifauna). In what follows, we illustrate stability properties analytically for the case of no agriculture. The dynamic system that arises under the case with agriculture is highly nonlinear, so an analytic presentation is not possible. Instead, the results are derived numerically in Table B1.

### Determinant

The determinant  $D$  of the Jacobian is

$$(B1) \quad D = 1 + \alpha r - \frac{\alpha S}{\beta q l k} - \frac{\alpha r S}{\beta q l k} = 1 + \alpha r - \frac{\alpha S}{\beta q l k} (1 + r).$$

Using Nerlove's (1993) Figure 1 as a guide, we want to know if  $D > 0$  and if  $|D| < 1$ . First,

consider the sign of  $D$ . Given that  $x = \frac{S}{\beta q l}$  (and hence  $D = 1 + \alpha r - \frac{x}{k} \alpha (1 + r)$ ) and

assuming  $\alpha < 1$ , we can show that  $D > 0$ . If  $\alpha < 1$  (and also since  $x < k$  by definition), then

$1 + \alpha r > \alpha(1 + r) > \frac{x}{k} \alpha(1 + r)$ . Subtracting the far RHS of this expression from the LHS, we

have  $D = 1 + \alpha r - \frac{x}{k} \alpha(1 + r) > 0$ .

$D > 0$  implies that we are above the horizontal axis in Nerlove Fig. 1. We now want to determine the conditions under which  $D < 1$ . The condition  $D < 1$  implies that

$r - \frac{x}{k} (1 + r) < 0$ , or, alternatively,  $r - \frac{S}{\beta q l k} (1 + r) < 0$ . Another way to write this is

$$(B2) \quad \frac{1 + r}{r} > \frac{\beta q l k}{S} = \Omega^{-1}.$$

The RHS is the maximum (but unsustainable) possible per capita meat intake ( $\beta q l k$ ) divided by the per capita subsistence level. Assuming a viable human population, the RHS (or  $\Omega$ ) must be greater than one. Rewrite (B2) as

$$(B3) \quad r < \frac{\Omega}{1 - \Omega}.$$

Hence, we find that the condition  $D < 1$  is satisfied for sufficiently small values of  $r$  (or for sufficiently large values of  $S$ , or sufficiently small values of  $\beta$ ,  $q$ ,  $l$ , or  $k$ , or both).

#### *Trace*

The trace of the Jacobian is

$$(B4) \quad T = 2 - \alpha \frac{S}{\beta q l k} = 2 - \alpha \frac{x}{k}.$$

With  $\alpha < 1$ ,  $T \in (1, 2)$ . It is also useful to know if  $D > T - 1$ . We can show this is the case,

$$(B5) \quad D - (T - 1) = 1 + \alpha r - \frac{x}{k} \alpha (1 + r) - ([2 - \alpha \frac{x}{k}] - 1) = \alpha r (1 - \frac{x}{k}) > 0.$$

Condition (B5) along with the condition  $D > 0$  rules out the possibility of a saddle equilibrium.

#### *Discriminant*

The discriminant of the Jacobian matrix of the planar system is

$$(B6) \quad \delta = \alpha^2 \Omega^2 + 4\alpha r [\Omega - 1],$$

where  $\Omega = \frac{S}{\beta q l k} < 1$ . The discriminant will be negative if the following condition holds:

$$(B8) \quad \frac{\alpha}{4r} < \frac{1 - \Omega}{\Omega^2}.$$

Given the results above for  $D$  and  $T$ , we find that the solution will be an unstable focus when  $r$  is sufficiently large (i.e.,  $D > 1$  and  $\delta < 0$ ), but if  $r$  is not too large and  $\alpha$  is sufficiently small, then a stable focus will emerge (i.e.,  $D < 1$  and  $\delta < 0$ ). Alternatively, if  $r$  is small and/or  $\alpha$  is large, then a stable node will arise (i.e.,  $\delta > 0$ ).

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<sup>26</sup> Nerlove (1993) also contains a useful graphical method to study the global dynamics of a planar system. This method confirms the patterns obtained using our numerical simulation method.

### *Implications*

Given that  $D > 0$ ,  $T \in (1,2)$ , and  $D - (T - 1) > 0$ , the solution can be one of three types: (i) stable focus ( $\delta < 0$ ,  $D < 1$ ; region II in Figure 1 Nerlove (1993)), (ii) unstable focus ( $\delta < 0$ ,  $D > 1$ ; region I), or (iii) stable node (with monotone path) ( $\delta > 0$ ,  $D < 1$ ; the part of region III that lies in the northeast quadrant). Hence, the steady state of the planar system is locally stable (node or focus) when  $D < 1$ .

In Table B1, we report the stability properties for all of the scenarios reported in Table 1 and Table 2. In each scenario, condition (B3) is satisfied so local stability is guaranteed. Note the determinant of the Jacobian for the megafauna model is close to unity. When  $D = 1$ , the equilibrium would be a nonhyperbolic fixed point (see Nerlove 1993, p.61).

In the case of megafauna (with no minifauna), the type of equilibrium is almost always a focus (except for the case of  $S=2$ ). Thus, overshooting would be possible under each parameter scenario, depending on the starting values of humans and megafauna, but again, we don't find this to be the case given the starting values we considered. In the case of minifauna (after megafauna have gone extinct), we find the equilibrium can be either a focus or a node. Overshooting is less likely in the minifauna case.

Table 1: Simulation results from model of megafauna and agriculture

Scenario	$N^*$ ( $\times 10^6$ )	$x^*$ ( $\times 10^6$ )	Percent of time hunting	Percent of time in ag.	Does extinction occur en route to the steady state?
<b>Benchmark</b> (diminishing returns to agriculture)	0.31	7.25	47.8	8.16	No
<b>Alternative Agricultural Scenarios</b>					
No agriculture ( $\mu=0$ )	0.25	7.98	60	--	No
Constant Returns to Scale Agriculture ( $\eta=1$ , $\mu=0.0055$ )	0.25	7.98	60	0	No
<b>Sensitivity Analysis</b>					
$\beta = 0.8$	0.32	4.57	48.7	25.2	No
$S = 2$	0.52	4.41	30	20	No
$q = 1.104 \times 10^{-10}$	0.24	5.45	47.8	8.16	No
$l=9,709$	0.32	5.02	36.2	15.95	No
$\mu=0.06$	0.41	6.68	36.2	15.95	No
$r=0.059$	0.32	7.25	47.8	8.16	No
$k = 50.25$ million	0.30	7.25	47.8	8.16	No
$\alpha = 0.067$	0.21	7.25	47.8	8.16	No

$N^*$  and  $x^*$  define steady state populations of early humans and megafauna, respectively. The benchmark scenario is defined by the parameter values  $S=2.9$  AU,  $q = 8.3 \times 10^{-11}$ ,  $r = 0.0443$ ,  $\beta = 0.6$ ,  $l=7300$ ,  $k=75$  million AU,  $\alpha=0.1$ ,  $\eta=0.45$ ,  $\mu=0.045$ ,  $N_0=100$ , and  $x_0=75$  million AU. In each of the other scenarios, all parameters except the one indicated are held constant at their benchmark scenario values.

Table 2: Simulation results from model of megafauna, agriculture, and minifauna

Scenario	Do megafauna go extinct?	Years till megafauna extinction	$N^*$ ( $\times 10^6$ )	$z^*$ ( $\times 10^6$ )	Percent of time hunting	Percent of time in ag.
<b>Benchmark</b> (diminishing returns to agriculture)	Yes	297	1.05	7.25	47.8	8.2
<b>Alternative Agricultural Scenarios</b>						
No agriculture ( $\mu=0$ )	Yes	296	0.81	7.98	60	--
Constant Returns to Scale Agriculture ( $\eta=1$ , $\mu=0.0055$ )	Yes	296	0.81	7.98	60	0
<b>Sensitivity Analysis</b>						
$\beta = 0.402$	Yes	346	1.12	11.58	36.2	2.3
$S = 3.857$	Yes	320	0.82	10.06	53.3	4.5
$q = 5.56 \times 10^{-11}$	Yes	381	1.04	7.25	47.8	8.2
$l = 4,891$	Yes	344	1.12	11.41	54.7	3.6
$r = 0.03$	Yes	408	1.05	7.25	47.8	8.2
$k = 99.75$ million	Yes	294	1.05	7.25	47.8	8.2
$\alpha = 0.133$	Yes	313	1.05	7.25	47.8	8.2
$h = 20.1$ million	Yes	323	0.88	7.25	47.8	8.2
$\alpha' = 0.268$	Yes	361	0.70	7.25	47.8	8.2
$q' = 1.104 \times 10^{-10}$	Yes	319	0.85	5.45	47.8	8.2

Note:  $N^*$  and  $z^*$  define steady state populations of early humans and small prey, respectively. The benchmark scenario is defined by the parameter values  $S=2.9$  AU,  $q = q'=8.3 \times 10^{-11}$ ,  $r = 0.0443$ ,  $\beta = 0.6$ ,  $l=7300$ ,  $k=75$  million AU,  $\alpha=0.1$ ,  $\eta=0.45$ ,  $\mu=0.045$ ,  $h=30$  million AU,  $\gamma=0.4$ ,  $N_0=100$ ,  $x_0=75$  million AU, and  $z_0=30$  million AU. In each of the other scenarios, all parameters except the one indicated are held constant at their benchmark scenario values.

Table B1. Stability Properties of the Scenarios from Table 1 and Table 2.

Scenario	Model					
	Megafauna Model (No Minifauna)			Minifauna and Megafauna Model (with Megafauna Extinct)		
	$D$	$\delta$	Stability Properties	$D$	$\delta$	Stability Properties
<b>Benchmark</b> (diminishing returns to agriculture)	0.95	-0.01	stable focus	0.77	0.012	stable node
<b>Alternative agricultural scenarios</b>						
No agriculture ( $\mu=0$ )	0.99	-11.7	stable focus	0.84	-0.05	stable focus
Constant returns to scale agriculture ( $\eta=1$ )	0.99	-11.7	stable focus	0.77	0.012	stable node
<b>Table 1 Scenarios</b>						
$\beta = 0.8$	0.9	-0.003	stable focus	----	----	----
$S = 2$	0.82	0.02	stable node	----	----	----
$q = 1.104 \times 10^{-10}$	0.95	-0.01	stable focus	----	----	----
$l = 9,709$	0.9	-0.005	stable focus	----	----	----
$r = 0.059$	0.95	-0.02	Stable focus	----	----	----
$k = 50.25$ million	0.95	-0.01	stable focus	----	----	----
$\alpha = 0.067$	0.97	-0.008	stable focus	----	----	----
<b>Table 2 Scenarios</b>						
$\beta = 0.402$	----	----	----	0.79	0.009	stable node
$S = 3.857$	----	----	----	0.82	-0.005	stable focus
$l = 4,891$	----	----	----	0.08	0.007	stable node
$r = 0.03$	----	----	----	0.77	0.03	stable node
$h = 20.1$ million	----	----	----	0.75	0.03	stable node
$\alpha' = 0.268$	----	----	----	0.85	-0.005	stable focus
$q' = 1.104 \times 10^{-10}$	----	----	----	0.79	0.002	stable focus

Note: For the Table 2 scenarios, we do not include scenarios involving  $q$ ,  $k$ , or  $\alpha$  because although these parameters affect the possibility of megafauna extinction, they do not affect the stability of the resulting steady state after megafauna have gone extinct.



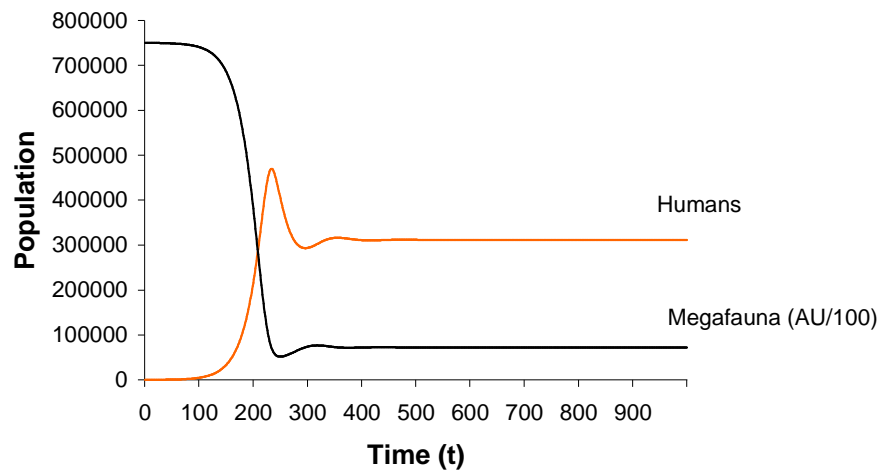


Figure 1. Time paths of human and megafauna populations with agriculture as the only  
alternative: co-existence of predator and prey

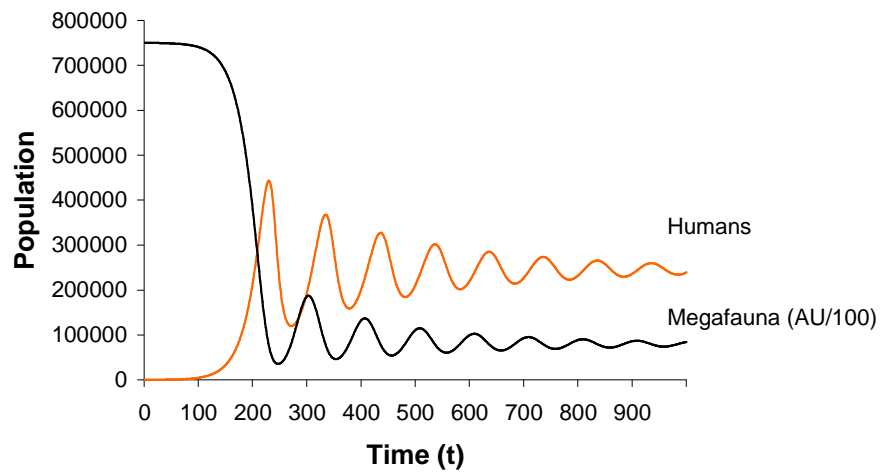


Figure 2. Time paths of human and megafauna populations: no agriculture

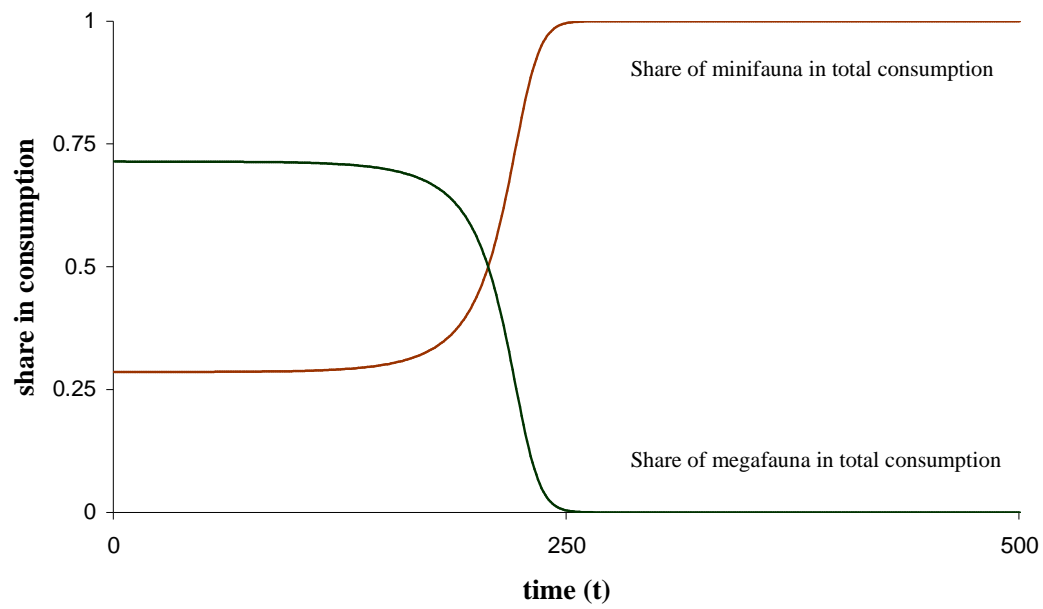


Figure 3. The Share of Minifauna and Megafauna in Consumption Over Time